

THE STRATIGRAPHICAL DISTRIBUTION AND TAXONOMY OF THE TRILOBITE *ONNIA* IN THE TYPE ONNIAN STAGE OF THE UPPERMOST CARADOC

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ABSTRACT. The litho- and biostratigraphy of the type section of the Onnian Stage in the Onny River, south Shropshire, is reassessed on the basis of detailed sampling over an extended period, including years when the river level was unusually low. The base of the Onny Formation is redefined at a level within the upper part of the Onnian and thus the base of the stage lies within the Acton Scott Formation. Four biozones are defined on the basis of closely spaced samples of the trinucleid trilobite *Onnia*, a peri-Gondwanan immigrant. In ascending order these are: the *O. superba cobboldi* Local Range Zone, the *O. s. creta* Local Range Zone, the *O. gracilis* Acme Zone, and the *O. s. superba* Local Range Zone. The second of these is based on a new subspecies, the others on a reassessment of previously named taxa. Within the *O. superba* subsp. zones, fringe pit distribution of successive samples of *Onnia* shows considerable stasis, although early and late populations of *O. s. superba* can be recognized. The changes between the subspecies can be viewed as reflecting either an evolutionary lineage or subtle fluctuations in environmental controls on a cline or set of ecophenotypes within a variable species.

THE richly fossiliferous type Caradoc succession of south Shropshire has been the subject of considerable interest since the publication of Murchison's *Silurian System* in 1839 (see Hurst 1979*a*, pp. 185–189 for historical review). Most importantly, as befits an international standard section, detailed work by Bancroft (1929–1949), Dean (1958–1964), and Hurst (1979*a, b*) has contributed significantly to the stratigraphy, trilobite and brachiopod systematics, sedimentology, and palaeoecology of the Shropshire Caradoc. However, there are still major problems with the definition of the uppermost (Onnian) stage and the correlation potential of its zone fossils, species of the trinucleid trilobite *Onnia*.

The present study addresses these problems and is based on mapping and annual sampling of the type Onnian section in the Onny River [Grid Ref. SO 425 854] between 1974 and 1983. This included some years when the water level was anomalously low and enabled bulk samples to be taken from horizons which were inaccessible to previous workers; in all, twenty-three levels have been extensively sampled. Bancroft also collected from this section and his sample points were well localized on a sketch map (Bancroft 1949, fig. 39). These samples, along with his original map and detailed field notes, are housed in the British Museum (Natural History), as is Hurst's collection. Comparison of these earlier samples with our own has proved most illuminating. For reasons of site conservation, our map is not reproduced in this paper but copies are available for consultation by bona fide researchers at the Hunterian Museum, Glasgow, British Museum (Natural History), and National Museum of Wales, Cardiff.

The present work demonstrates that the base of the Onnian stage does not correspond to a clear lithological change in the Onny River section (cf. Hurst 1979*a, b*) and we draw a much clearer distinction between litho-, bio-, and chronostratigraphy than did some earlier workers. Moreover, assessment of the successive changes in samples of *Onnia* enables a revised set of biozones for the type Onnian to be established. These samples also provide a case study demonstrating the

difficulties of distinguishing between evolutionary and ecophenotypic/clinal variation in a series of populations at a single site.

THE TYPE ONNIAN STAGE

The term Onnian was introduced by Bancroft for the uppermost stage of the Caradoc Series in his privately published correlation tables (1933). These show that Bancroft placed the base of the stage below the 'Fossil-bed with *O[mmia] cobboldi*' in the Onny River section. This latter horizon was undoubtedly his locality Px (see Bancroft 1949, fig. 39; also text-fig. 1 herein). Bancroft recognized three zones within the Onnian characterized by, in ascending order: *O. cobboldi*, *O. gracilis*, and *O. superba*. All three species were named by him in 1929 (Bancroft 1929*b*) and referred to his new genus *Onmia* in 1933.

O. gracilis has also been described from Welshpool in the Welsh Borderlands (Cave 1965) and the Cross Fell Inlier in northern England (Dean 1962). The occurrence at Welshpool is in association with a similar binodicope ostracod fauna to that in the Onny River (Jones 1987, p. 108). At Cross Fell *O. gracilis* is succeeded by '*O. s. pusgillensis*' Dean, 1961 which also occurs in the uppermost Onnian of nearby Cautley (Ingham 1966, 1974). Thus, Bancroft's *O. gracilis* Zone has been at least tentatively recognized outside the type area and '*O. s. pusgillensis*' has been considered to indicate the *O. superba* Zone in northern England (but see below p. 853).

The base of the type Onnian is defined primarily on the first appearance of '*O. cobboldi*' (see below for revised taxonomy) at a level about 6 m below Bancroft's locality Px (text-fig. 1). There are also changes in several other elements of the shelly fauna as detailed by Dean (1963, pp. 8, 13–14) and Hurst (1979*b*, p. 212). Of particular interest for international correlation (e.g. Owen 1980, 1987) is the occurrence of another trinucleid trilobite, *Tretaspis ceriodes* Angelin *favus* Dean at levels immediately above and below this boundary (Dean 1963, p. 8). Another subspecies, *T. c. alyta* Ingham, occurs in the uppermost Onnian of northern England (Ingham 1970, pp. 50, 52).

The Onnian strata in Shropshire are overstepped eastwards, with small angular unconformity and overlap, either by the upper Llandovery Hughley Shale Formation (as in the Onny River section) or by the underlying Pentamerus Beds to the north-east. However, a continuous succession is present at Cautley where the base of the Pusgillian Stage (and therefore the base of the Ashgill Series) is defined (Ingham 1966; Ingham and Wright 1970; Wright *in* Whittington *et al.* 1984). This boundary is marked (*inter alia*) by the disappearance of *Onmia* from Britain and the first appearance of members of the *T. seticornis* species group.

The precise correlation of the Onnian Stage with the standard graptolite and conodont zones remains unclear. Present evidence suggests that the stage may equate with the uppermost *D. clingani* and most of the *P. linearis* graptolite zones (Ingham and Wright 1970; Wright *in* Whittington *et al.* 1984). The base of the *A. ordovicicus* conodont zone may also lie within the stage (Savage and Bassett 1985, p. 683) in spite of statements to the contrary (Orchard 1980; Bergström and Orchard 1985).

REVISED BIOSTRATIGRAPHY

Bancroft's work on the upper Caradoc faunas of the Onny River section was based on bulk samples taken from exposures on the river bank. In the Onnian Stage, these samples were widely spaced (Bancroft 1949, fig. 39) and give only a broad picture of the biostratigraphy. The present study involves more closely spaced samples, many from the river bed (text-fig. 1). Nevertheless, Bancroft's material was so well localized that it can be easily accommodated in our analysis.

The zone fossils of the Onnian Stage, species of *Onmia*, belong to a group of trilobites with a cephalic fringe which is pitted in a regular and quantifiable pattern (see Hughes *et al.* 1975 and text-fig. 2 herein). This pitting is widely used taxonomically and even poorly preserved fringe fragments can yield useful data. Where the trilobites are sufficiently abundant (as in the type Onnian), statistical analysis of fringe pit distribution can be used to assess sequential changes

in populations. They also allow a semi-quantitative rather than purely typological definition of taxa.

The successive changes in samples of *Onnia* from the Onny River are discussed in detail below. It is clear that whilst *O. gracilis* is distinctive there is considerable overlap in pit distribution and gross morphology in the ranges of variation of *O. superba* and *O. cobboldi* from their type horizons. These latter taxa are redefined as subspecies of *O. superba*; their definitions encompass samples from other horizons near the top and base of the type Onnian (text-figs. 1, 3, 4). A third subspecies, *O. s. creta* subsp. nov. is here established both in terms of pit distribution and fringe shape for the samples from horizons immediately below those containing *O. gracilis*. Lacking any evidence on the occurrence of these three subspecies of *O. superba* outside the Onny River, we take a cautious view of their correlative potential. Nevertheless, the type Onnian is here redefined as comprising four biozones (text-fig. 1) in ascending order: the *O. s. cobboldi* Local Range Zone, the *O. s. creta* Local Range Zone, the *O. gracilis* Acme Zone, and the *O. s. superba* Local Range Zone.

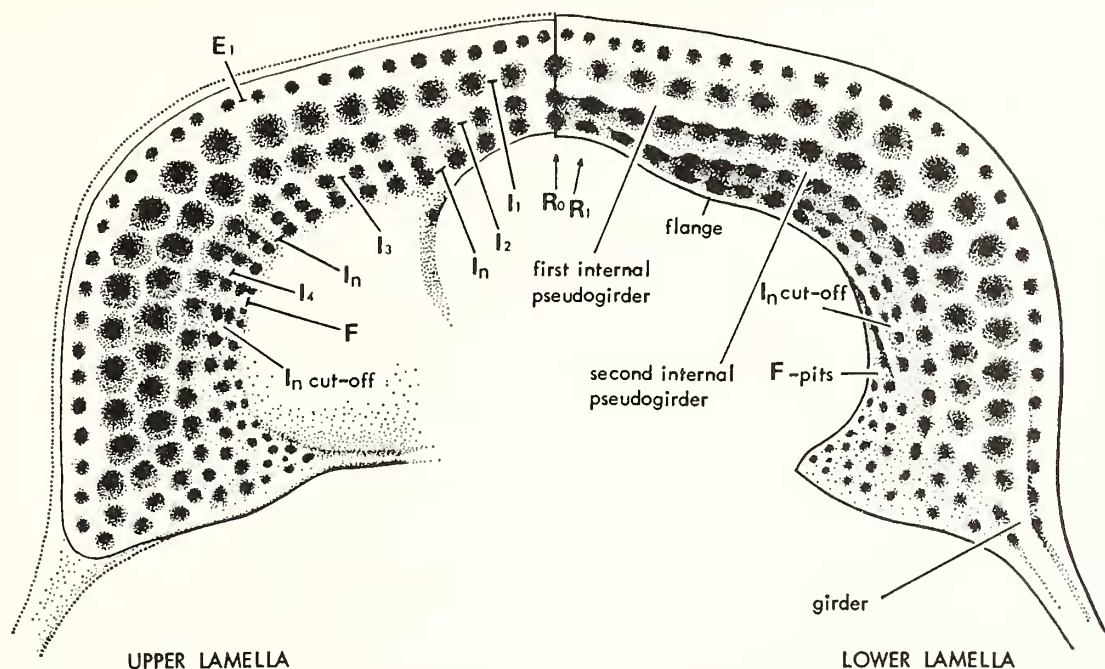
The bases of all four zones are defined on the first occurrence of the eponymous species or subspecies. *O. gracilis* persists as a rare element of the earliest *O. s. superba* Zone and hence the underlying strata, where *O. gracilis* is abundant, are defined as an acme zone. The occurrence of *O. gracilis* at Welshpool and Cross Fell may be at a broadly similar level to its presence in the type Onnian but this is poorly constrained. *O. gracilis* also occurs at Cardington, Shropshire along with specimens of *T. ceriodes* which are morphologically closer to *T. c. alyta* and a morph of *T. c. angelini* Störmer than to *T. c. favius*. Owen (1980, p. 722) suggested that the strata here may be Onnian in age but the presence of *Flexicalymene salteri* Bancroft and the brachiopods *Onniella depressa* Bancroft (*sensu* Hurst 1979b) and *Chonetoides cf. radiatula* (Barrande) (D. A. T. Harper, pers. comm. 1987) now confirm the Actonian age given by Dean (1963, pp. 8–9). Hurst (1979b, p. 204) noted that *O. depressa* appears high in the Actonian Stage in the Onny Valley and thus the strata at Cardington may be equivalent to this level. None the less, it appears that *Onnia gracilis* ranges both above and below its Acme Zone.

The taxonomic affinities of *O. s. pusgillensis* Dean in northern England are unclear and may even be closer to *O. gracilis* than to *O. superba*. It is therefore regarded as a distinct species, *O. pusgillensis* (see text-fig. 2).

LITHOSTRATIGRAPHY

Hurst (1979b, figs. 2, 3, 11) summarized the historical development of the terms applied to the type upper Caradoc and established a modern lithostratigraphical terminology. He assigned all the strata of Onnian age to the 'Onny Shale Formation'—a usage which broadly followed that of (*inter alia*) La Touche (1884, 'Onny Shales') and Dean (1958–1963, 'Onnia Beds'). In contrast, Bancroft (1929b, 1933) restricted the terms 'Trinucleus Shales' or 'Onny Shales' to the uppermost Onnian Stage, assigning the lower Onnian to the underlying 'Acton Scott Beds'. He placed the base of the latter at about the Marshbrookian–Actonian boundary (cf. Hurst 1979b, fig. 2). Hurst (1979b, p. 178) defined the Onny Shale Formation in the Onny River as comprising 20 m of bioturbated, very fossiliferous blue-black mudstones overlain by 5 m of laminated blue-grey mudstone succeeded by yellow-weathering blocky mudstones of the river cliff section (perhaps another 18 m). He defined the base of the Onny Shale Formation as lying in a 3 m gap in exposure below which are the poorly fossiliferous calcareous mudstones and siltstones of the Wistanstow Member of the Acton Scott Formation. Hurst termed the Onnian fauna the '*Onniella broeggeri*–*Sericoidea homolensis* Association' and considered it to have lived in a distal shelf setting (1979a, pp. 223–228, 238–239).

Hurst sampled twenty-six horizons in his Onny Shale Formation (1979a) but our analysis of his samples in the British Museum (Natural History) shows that only the lowest two (thought by Hurst to be from the lowest 2.5 m of the unit) contain *Onnia superba cobboldi*. The succeeding five samples contain *O. s. creta* and the next five *O. gracilis*. The highest of these (no. 32), from



TEXT-FIG. 2. The fringe in *Onnia pusgillensis* Dean (as redefined herein) shown diagrammatically as corresponding upper and lower lamellae and labelled to show the location of pit arcs and other fringe features discussed herein. Original illustration of Ingham (1974, text-fig. 20), published by kind permission of the Palaeontographical Society.

c. 15 m above the base of Hurst's section, also contains *O. s. superba* which persists through the rest of the sequence. There is no doubt, therefore, that the lowest 10 m of the Onnian was not sampled by Hurst who underestimated the stratigraphical thickness between his lowest sample and those yielding Actonian faunas. This unsampled part of the sequence constitutes most of the *O. s. cobboldi* Zone, including the type horizon of the eponymous subspecies (Px of Bancroft, sample B herein).

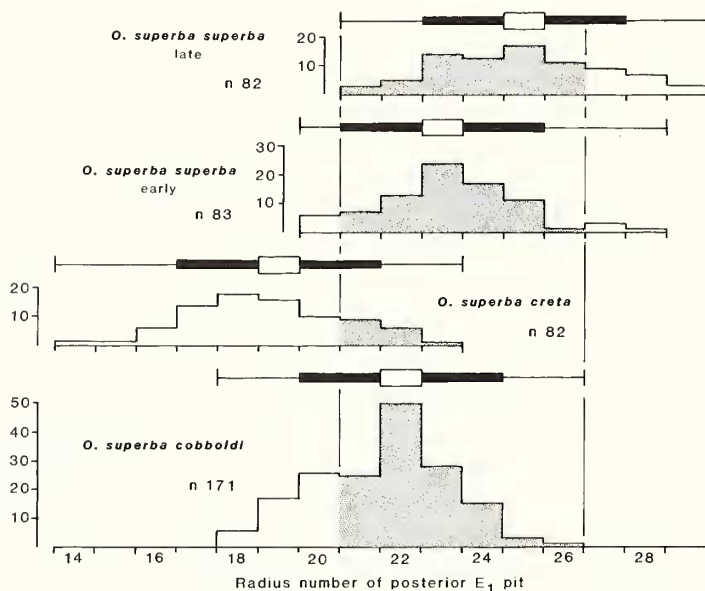
The rubbly, calcareous lower Onnian strata show a greater lithological similarity to the underlying Wistanstow Member of the Acton Scott Formation than to the overlying blocky mudstones and are here included in the lower unit (text-fig. 1). The base of the laminated blue-grey mudstone noted by Hurst is here taken as the base of the Onny Formation and lies within the *O. s. superba* Local Range Zone. As only this lowest c. 5 m is at all shaly, we recommend that the term 'shale' be omitted from the formation name.

At sample locality O in the lower part of the *O. s. superba* Zone (uppermost Acton Scott Formation as herein understood) the rubbly mudstones contain largely comminuted shelly debris and more complete specimens are rare. Nevertheless, this 5 cm horizon is particularly interesting in that it contains abundant, hard irregularly shaped phosphatic nodules in which the fine shelly debris is well preserved. The episode of slow deposition represented by this horizon may be broadly coeval with similar events which also produced bands of phosphate nodules in, for example, the Nod Glas and Blaen y Cwm formations in mid Wales.

ONNIA IN THE TYPE ONNIAN

Onnia was a late Caradoc immigrant into the British area and stayed but a short time. Its origins were in higher latitudes around Gondwanaland where it has a much greater stratigraphical range

(early Caradoc to Ashgill; Hughes *et al.* 1975, p. 575). It was derived from another middle Ordovician marrolothine, *Deanaspis*, which is not known from the British Isles (see Hughes *et al.* 1975). The appearance of *Onnia* in Shropshire may reflect the circulation of cold, fairly deep waters of the outer neritic regime which was the climax of the Caradoc transgression in the area. This correlates with the widespread Nod Glas deepening in mid Wales and with the probable circulation of colder waters at even greater depths which brought a peri-Gondwanaland cyclopygid biofacies to the margins of Laurentia at Girvan—the Upper Whitehouse Group (Ingham 1978). Specimens of *Onnia* far outnumber the relatively few other trilobites at most levels in the type Onnian and thus provide an effectively continuous record of the genus in Shropshire over a period in excess of a million years.



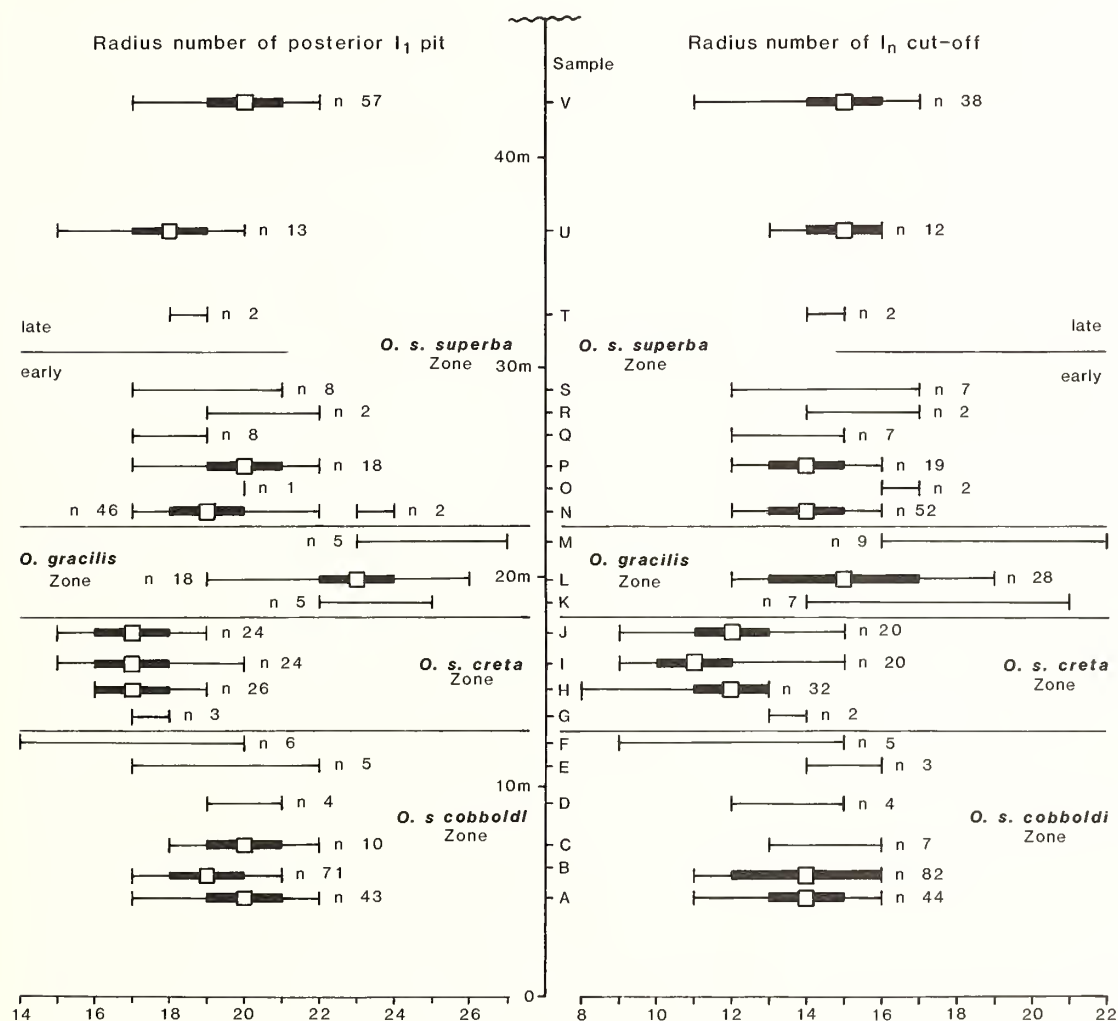
TEXT-FIG. 3. Histograms showing the radius number of the posterior E₁ pit in pooled samples of the successive subspecies of *Onnia superba* highlighting the overlap (shaded) between *O. s. cobboldi* and samples of *O. s. superba* from the highest part of the Onny River section. Both of these histograms include data from the Bancroft Collection.

The revised zonation of the type Onnian is founded on the successive appearance, without overlap, of three subspecies of *O. superba*; the second and third of these being separated by the only distantly related *O. gracilis*. The fringe pits enable a semi-quantitative, graphical assessment of successive changes between population samples of the same taxon and between taxa. These changes are not size dependent; pit distribution in an individual becomes fixed at an early stage in ontogeny, as was also demonstrated by Hughes (1970). The gross changes between the subspecies of *O. superba* in all the pit arcs are shown on text-figs. 3 and 5, whilst the text-figs. 1 and 4 also illustrate the range, mean, and one standard deviation on each side of the mean for arcs E₁, I₁, and I_n in each sample. These three arcs extend around the whole fringe and are the outermost arc (E₁), innermost arc (I_n), and first arc inside the girder (I₁) (see Ingham 1974, pp. 59–60 for fringe pit terminology in *Onnia*; Hughes *et al.* 1975). All values refer to half-fringe counts and only the range is given in very small samples. Table 1 shows changes from sample to sample in arcs I₂, I₃, and the F pit series in the subspecies of *O. superba*.

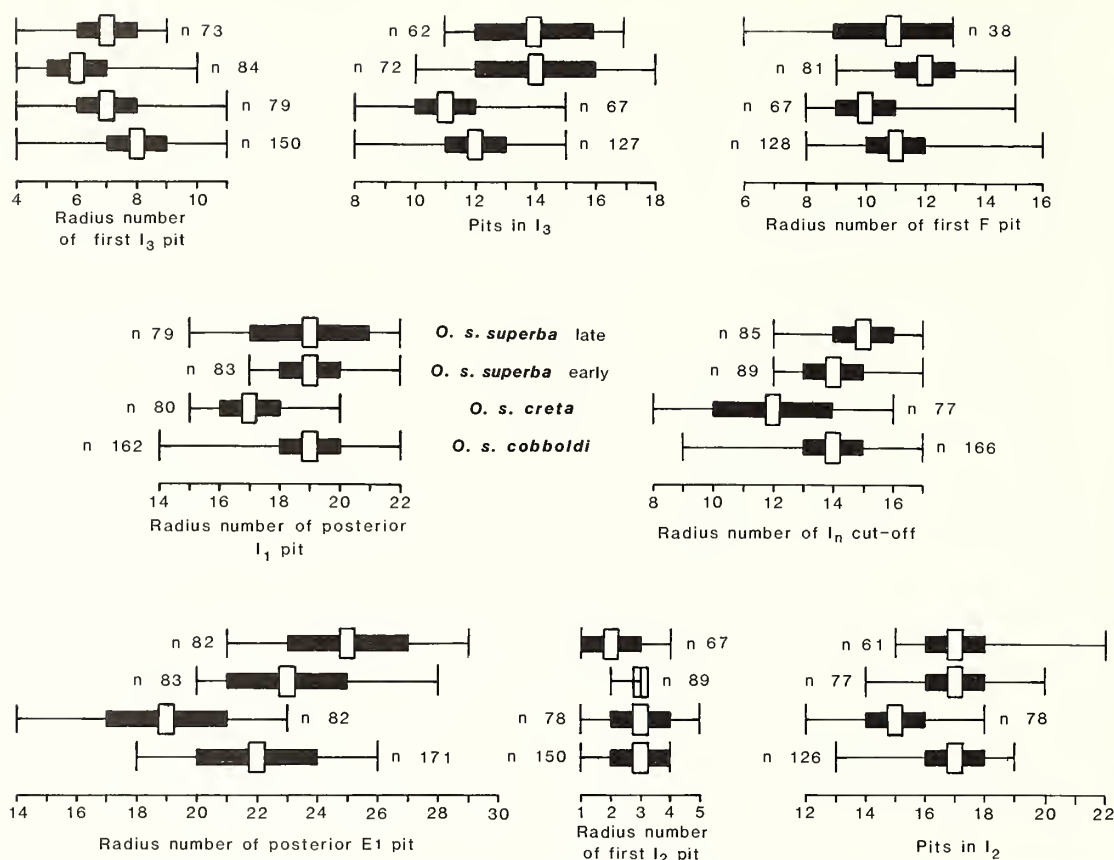
Successive changes in the type Onnian

The earliest subspecies, *O. s. cobboldi*, shows stasis in all its fringe characters except for the stratigraphically highest sample which shows a reduction in pit number. This heralds *O. s. creta*, which is also characterized by a strongly inflated area of the posterior fringe along the I_1 arc—a feature seen only in a subdued form in some specimens of *O. s. cobboldi*. Chi-squared tests show that the reduction in pit number in *O. s. creta* compared with the earlier subspecies is significant at less than the 0.1% probability level for arcs E_1 , I_1 , I_n , and I_2 . Most arcs show little or no change from sample to sample in *O. s. creta* but the mean number of pits in arcs E_1 and I_2 shows a progressive decrease, effectively continuing the 'trend' from *O. s. cobboldi*.

The sequence of *O. superba* populations is interrupted by the appearance of *O. gracilis*, a very



TEXT-FIG. 4. Changes in the radius numbers of the posterior I_1 pit and the I_n cut-off in successive samples of *Onnia* from the type Onnian Stage. Range, mean, and one standard deviation on each side of the mean shown for the larger samples. Note that each taxon is restricted to its own zone except that a few specimens of *O. gracilis* occur with the lowest sample of *O. superba* and these provided the two high pit counts in arc I_1 . Sample V incorporates specimens from the Bancroft Collection.



TEXT-FIG. 5. Summary of the fringe pit distribution in the subspecies of *Onnia superba* in the type Onnian Stage showing range, mean, and one standard deviation on each side of the mean. The samples of *O. s. cobboldi* and late *O. s. superba* include specimens from the Bancroft Collection.

different species in several respects; of the features depicted on text-figs. 1 and 8, the most substantial difference is shown by arc E_1 . The very large number of pits in this arc exceeds even the upper end of the range in *O. superba*. Two morphs can be recognized within the samples of *O. gracilis* based on the presence or absence of arc I_4 . The percentage of individuals with this arc decreases upwards through the *O. gracilis* Acme Zone from 94 % (sample K, $n = 18$) through 91 % (L, $n = 43$) to 42 % (M, $n = 119$), although both specimens of *O. gracilis* in the lowest *O. s. superba* sample have this arc.

O. s. superba is closer to *O. s. cobboldi* than to *O. s. creta* not only in lacking the strongly inflated posterior part of I_1 but also in having a greater mean number of pits in every arc (text-fig. 5). There is therefore a reversal of the pit reduction that marks replacement of *O. s. cobboldi* by *O. s. creta*. This is further emphasized when successive samples of *O. s. superba* are analysed (e.g. text-figs. 1 and 4; Table 1). These fall readily into two groups. 'Early' populations (samples N-S) have a fairly planar fringe surface and a range and mean values for each pit arc equal to or slightly greater than those in *O. s. cobboldi*. In contrast, 'late' populations (T-V) have a more convex fringe surface and, in the case of arcs E_1 and I_n , an increased mean pit count. Chi-squared tests show that the numbers of pits in E_1 and I_2 in *O. s. cobboldi* and early *O. s. superba* are significantly different at the 0.1 % level. The same applies to E_1 and I_n when the early and late

TABLE 1. The range, mean (\bar{x}), and sample size (n) of selected fringe features of the successive samples of subspecies of *Omnia superba* from the Onny River section. Such changes in arcs E_1 , I_1 , and I_n are illustrated graphically on text-figs. 1 and 4. Sample V incorporates specimens from the Bancroft Collection.

Sample	Radius number of first I_2 pit			Pits in I_2			Radius number of first I_3 pit			Pits in I_3			Radius number of first F pit		
	Range	\bar{x}	n	Range	\bar{x}	n	Range	\bar{x}	n	Range	\bar{x}	n	Range	\bar{x}	n
<i>O. s. superba</i>															
Late															
V	1-4	2	56	15-22	18	51	4-9	7	60	11-16	14	50	6-13	11	31
U	2-3	—	9	17-18	—	8	6-8	7	11	11-17	14	10	10-13	—	6
T	2-3	—	2	17	—	2	5-7	—	2	14-15	—	2	8	—	1
Early															
S	3	—	7	14-19	—	7	6-9	—	6	10-15	—	7	9-14	—	5
R	3	—	2	16-19	—	2	6-7	—	2	17	—	1	11-14	—	2
Q	2-3	—	9	15-18	—	7	4-8	—	7	12-15	—	4	11-12	—	6
P	2-3	3	17	16-19	18	16	4-8	6	16	12-17	14	13	9-14	12	16
O	2	—	2	17-20	—	2	7-8	—	2	14	—	2	11-15	—	2
N	2-3	3	52	15-19	17	43	4-10	6	51	10-18	14	45	9-14	12	50
<i>O. s. creta</i>															
J	2-4	3	24	12-17	14	19	5-11	7	23	8-13	11	19	8-13	10	18
I	1-5	3	17	13-16	15	16	5-9	7	19	10-13	11	17	8-15	10	17
H	1-4	3	31	12-18	15	26	4-8	6	32	9-13	11	26	8-11	9	29
G	2	—	3	13-15	—	2	7-8	—	2	11	—	2	10	—	1
<i>O. s. cobboldi</i>															
F	2-3	—	5	14-17	—	5	4-8	—	5	13	—	4	8-12	—	5
E	2-3	—	3	18-19	—	2	6-7	—	2	13-15	—	2	11	—	2
D	3	—	2	17	—	2	8-9	—	3	11-13	—	3	11-12	—	3
C	2-3	—	7	14-18	—	6	7-9	—	7	12-16	—	6	11-13	—	6
B	1-4	3	75	14-19	16	65	5-11	8	69	9-14	12	61	9-14	11	63
A	2-4	3	35	13-19	17	28	5-10	8	41	10-14	12	35	9-14	12	30

samples of *O. s. superba* are compared. The change from early to late *O. s. superba* occurs at about the base of the Onny Formation as redefined herein.

In contrast to the general 'trends' in *O. superba* noted above, some fringe pit data show a more complex pattern of change. The position of the first F pit shows a marked zigzag series of changes (text-fig. 5). In contrast, the mean position of the first I_3 pit shows a significant adaxial shift from *O. s. cobboldi* through *O. s. creta* to early *O. s. superba*, but late *O. s. superba* shows a reversal of this 'trend'.

INTERPRETATION

The changes in pit number and distribution seen in the successive samples of *O. superba* include several which are (albeit significant) shifts in mean values largely within the considerable overlap in the range of values shared by the different subspecies. However, two features in particular indicate that the changes in the type Onnian are not simply random fluctuations in pit number within an essentially conservative species. First, successive samples of the same subspecies (or the early and late forms of *O. s. superba*) show a considerable degree of stasis in the range and mean values of most pit counts. Secondly, the range of values in the most variable fringe pit feature, the number of pits in E_1 , shows marked differences between subspecies (text-fig. 3). This is especially true in the case of *O. s. creta* in which only 19.5% ($n = 82$) of specimens have enough pits in E_1 to fall within the overlap in range between *O. s. cobboldi* and the late *O. s. superba*. Moreover, the admittedly small sample (F) from the top of the *O. s. cobboldi* Zone shows a downward shift in the number of pits in E_1 , and is therefore transitional towards the range seen in the slightly younger *O. s. creta*. Other pit counts (e.g. I_1 , I_n —see text-fig. 4) also show this transitional condition but the swelling along the lateral part of I_1 is much weaker than in *O. s. creta*.

If the changes seen in *O. superba* are not random fluctuations, they must reflect either an evolutionary lineage (or lineages) or fluctuations in environmental conditions affecting one very variable species whose morphology is ecologically controlled. As *O. superba* is unknown outside the type area there is insufficient evidence to confirm either hypothesis but, in view of the possible biostratigraphical importance of *Omnia*, some discussion and speculation is merited.

Evolution

The presence of *O. gracilis* and consequent gap in the record of *O. superba* in the middle of the type Onnian complicates any evolutionary interpretation of the *O. superba* subspecies. The change from the relative stasis of *O. s. cobboldi* to that of *O. s. creta* could be viewed as a punctuational event with only the youngest sample of *O. s. cobboldi* being intermediate in pit number if not fringe swelling. *O. s. superba* appears above the *O. gracilis* Zone and has a fringe shape and pit number in each arc that are closer to those of *O. s. cobboldi* than *O. s. creta*. This reversion to a higher pit count is continued in *O. s. superba* with the change from 'early' to 'late' populations. The rate of this change in *O. s. superba* cannot be assessed as it takes place in a poorly fossiliferous part of the sequence.

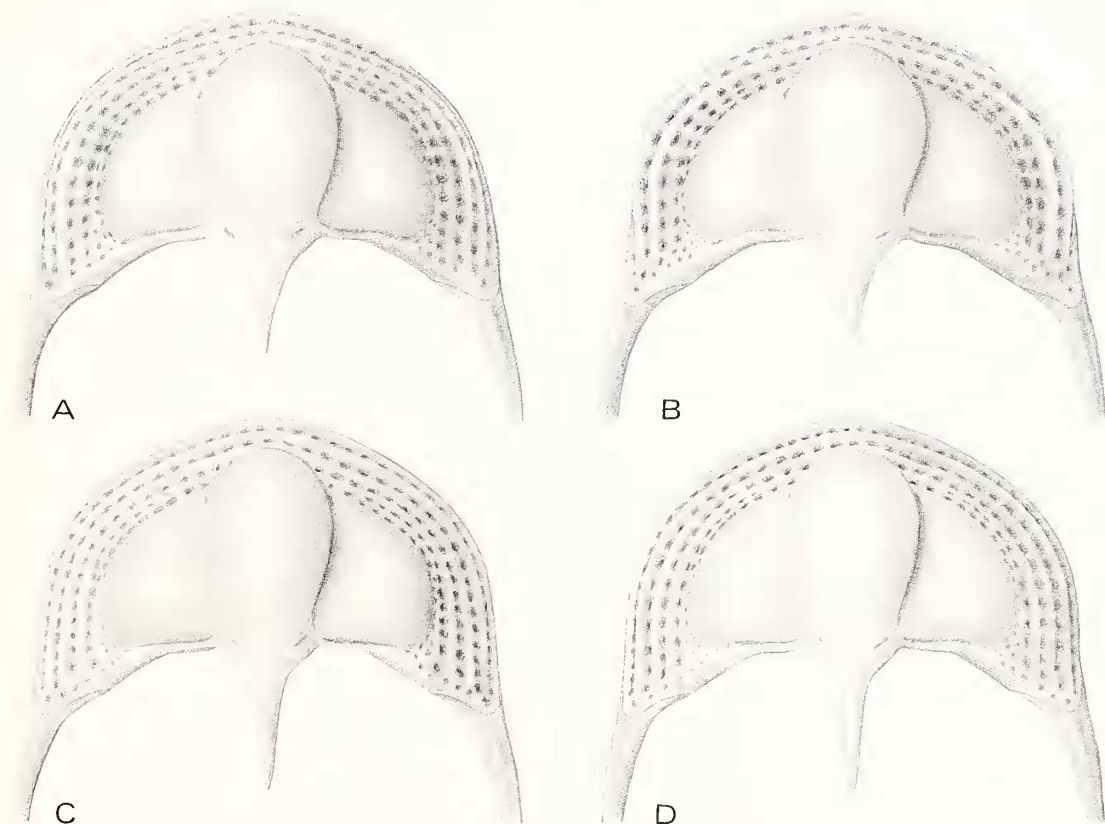
None of these changes is considered to be of sufficient magnitude to indicate the formation of a new species but they can be described in an analogous way. The *O. gracilis* interval masks the critical evidence which would indicate whether a single lineage or a branching event is represented in the evolution of *O. superba* (see text-fig. 1). In the former case, *O. s. superba* would have been derived from *O. s. creta* by a reversal of the earlier trend (= 'detour trend' of Henningsmoen 1964). Alternatively, *O. s. creta* may represent a side branch of an otherwise fairly conservative lineage from *O. s. cobboldi* to *O. s. superba*, a substantial part of which is not represented (for ecological reasons) in the Onny section. In either model, the appearance of *O. s. creta* (and possibly late *O. s. superba*) might best be viewed as an example of punctuated equilibria (Gould 1985 and references therein). In the single lineage hypothesis it would also conform to the 'punctuated gradualism' documented by Malmgren *et al.* (1983, 1984) in planktonic foraminifera. This was reinterpreted by Gould (1985, p. 10) as 'punctuated anagenesis' and reflects changes of short duration (but with

intermediates) separating periods of stasis but without lineage splitting. Maynard Smith (1983) has discussed the possible genetic controls on stasis and punctuation.

Ecological control

Both suggested evolutionary models for the changes in *O. superba* involve at least some ecological control on the presence or absence of particular subspecies, or even *O. superba* itself, in the type Onnian. An extreme development of this would be to regard the various subspecies as entirely ecologically controlled morphologies. This could be as portions of an intergradational cline distributed along an environmental gradient (e.g. Cisne *et al.* 1982) or as ecophenotypes developed in response to particular sets of environmental conditions (e.g. Mayr 1963; Johnson 1981; Hurst 1978, 1982 and references therein).

The only major lithological changes in the type Onnian are at the base of the Onny Formation where the sparsely fossiliferous laminated mudstone is developed and overlain by blocky mudstone. More subtle environmental controls (or selection pressures) must have operated earlier, yet it is in these lower three zones that a coherent (if simple) positioning of subspecies in a morphoseries can be postulated. Taking the two most variable features—the number of pits per arc (especially E_1) and the shape of the fringe—the series extends from *O. s. creta* with a low pit count and strongly swollen posterior fringe, through *O. s. cobboldi* with an increased pit count and gentle posterior



TEXT-FIG. 6. Reconstructions in dorsal view of cephalons of the three subspecies of *Onnia superba* recognized herein, showing typical morphological differences between them, *c.* $\times 3$. A, *O. s. cobboldi* (Bancroft). B, *O. s. creta* subsp. nov. C, *O. s. superba* (Bancroft), early form. D, *O. s. superba* (Bancroft), late form (which includes the type material of *O. s. superba*).

swelling, to early *O. s. superba* with a similar or even larger number of pits and a flatter fringe profile (text-fig. 6). The Onny River *O. superba* faunas began, therefore, in the middle of this morphoserries and after a period of stability were replaced, with slight gradation in terms of pit number, by the *O. s. creta* 'end member'. After another period of stability a much more profound environmental shift brought a different species, *O. gracilis*, into the area. This may reflect a deepening event as the broadly contemporaneous appearance of *O. gracilis* at Welshpool is thought to have been in response to the 'Nod Glas transgression' (Dean 1963; Cave 1965). Whatever the change was, it was sufficient for the 'early' *O. s. superba* morphology to be 'missed out'. The subspecies only appeared later with, and eventually completely replacing, *O. gracilis*—perhaps indicating a slight regression. The base of the Onny Formation and the broadly coeval appearance of late *O. s. superba* is associated with a depleted fauna that was interpreted by Hurst (1979a, pp. 231–232) as reflecting poorly oxygenated conditions caused by upwelling of oxygen-poor waters from deeper levels in the basin. Late *O. s. superba* shows an increased pit count and in this respect can be placed at the 'high' end of the postulated morphoserries. Its fringe profile, however, is closer to that of *O. s. cobboldi* than early *O. s. superba*, and thus does not fit this simple picture.

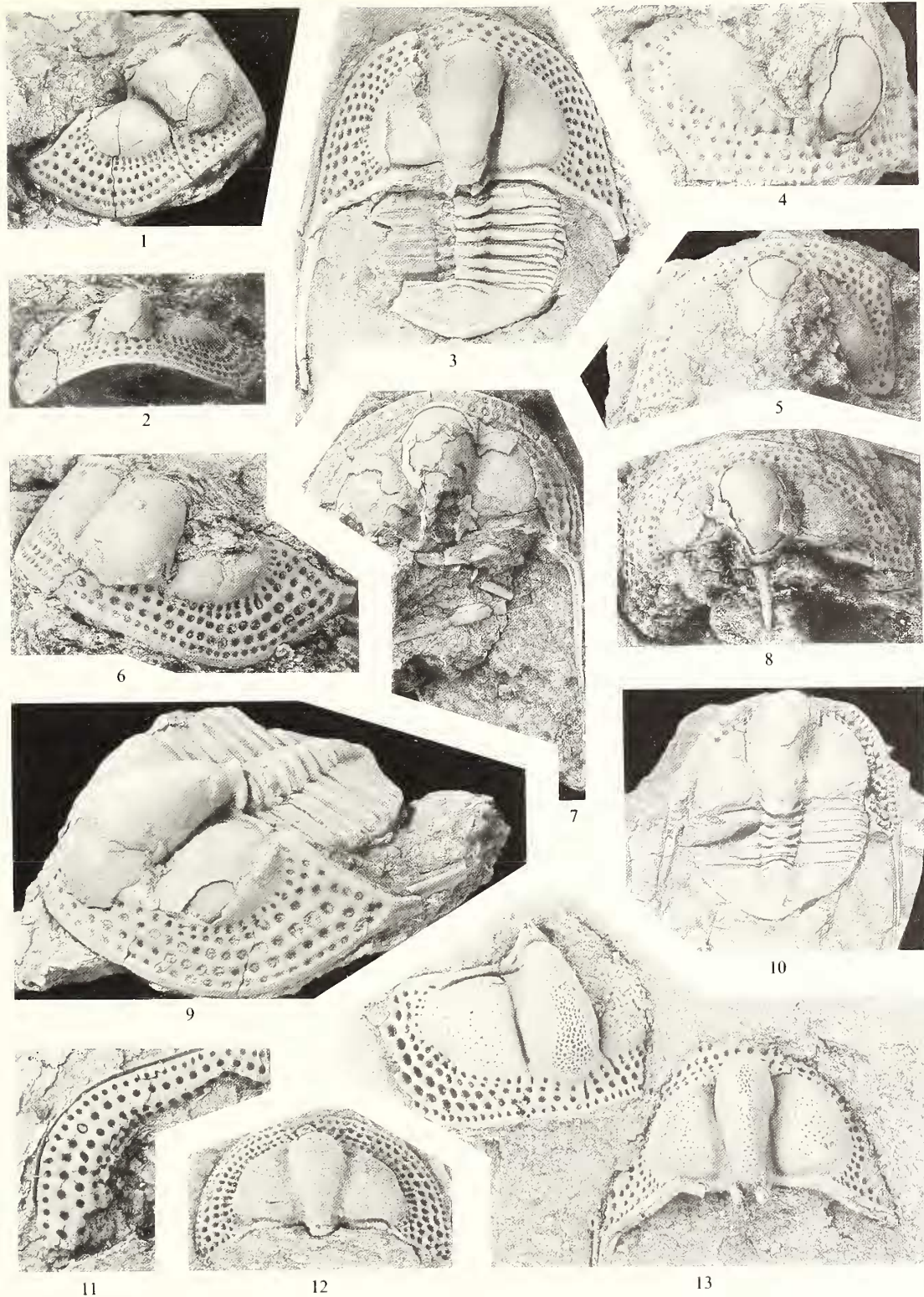
The subdivision of *O. superba* into subspecies adopted in this paper implies either a punctuated evolutionary explanation or at least discrete ecologically controlled, entities rather than arbitrary points along completely intergradational chronoclines, topoclines, or ecophenotypic series. The subdivision is, however, partly a pragmatic solution to the available data. Any of these hypotheses could be correct but they can only be tested if *O. superba* is found outside its type locality.

SYSTEMATIC PALAEOLOGY

The terminology used herein is that advocated by Ingham (1974; see also text-fig. 2 herein) and Hughes *et al.* (1975), and pit counts refer to half-fringe values. Although we cite ranges in variation in fringe pit distribution in diagnoses, we do not intend the values from our samples to be completely prescriptive. Thus the terms 'approximately' and 'about' are used in order to avoid (say) a specimen with one more pit in an arc being excluded from the taxon or a new diagnosis being required. Specimens are housed in the Hunterian Museum, Glasgow University (HM) and the British Museum (Natural History) (BM).

EXPLANATION OF PLATE 74

Figs. 1–13. *Onnia superba superba* (Bancroft) from the *O. s. superba* Local Range Zone, Onnian Stage, Onny River section, south Shropshire. Note that figs. 1–6, 8, 9 are from early populations and figs. 7, 10–13 from late populations. These are also from the uppermost Acton Scott and Onny formations respectively. All specimens testate or largely so unless otherwise stated. 1, BM In52011/1, oblique anterolateral view of cephalon, Bancroft Collection loc. Pc (equivalent to sample N herein), $\times 3$. 2, HM A15145, frontal view of cephalon, sample N, $\times 3$. 3, BM In49028, dorsal view of almost complete individual, Bancroft loc. Pc (= N herein), $\times 3$, figured by Dean (1960, pl. 19, fig. 1) as '*O.? cobboldi*' in the mistaken belief that it came from the type locality of that form (Bancroft's Px, our B); the specimen bears Bancroft's original loc. Pc label. 4 and 5, HM A21759, oblique anterolateral and dorsal views of cranidium showing healed severe damage to right side of fringe, sample N, $\times 3$ and $\times 4$ respectively. 6, HM A21758, oblique anterolateral view of cephalon, sample N, $\times 3$. 7, HM A21751, partially exfoliated cephalon with parts of three thoracic segments, sample U, $\times 2$. 8, HM A15148, dorsal view of partially exfoliated cephalon showing long occipital spine, sample P, $\times 3$. 9, HM A21741, oblique anterolateral view of complete individual sample N, $\times 3$. 10, BM In49029, dorsal view of exfoliated almost complete specimen with ventral mould of lower lamella of fringe; cliff section, $\times 1.5$, figured by Dean (1960, pl. 19, figs. 13 and 14). 11, HM A21757, internal mould of lower lamella of fringe, sample U, $\times 3$. 12, HM A21767a, dorsal view of rather flattened cranidium, cliff section, $\times 3$. 13, HM A21753b and HM A21754b, latex peel of external moulds of small cranidium and cephalon respectively, both showing broad reticulated band on mesial part of glabella, loc. U, $\times 6$.



Family TRINUCLEIDAE Hawle and Corda, 1847

Subfamily MARROLITHINAE Hughes, 1971

Genus ONNIA Bancroft, 1933

Type species. *Cryptolithus superbus* Bancroft, 1929b, p. 95, pl. 2, fig. 10, from the Onny Formation (as redefined herein), Onny River section, south Shropshire, England; by original designation.

Discussion. The recognition of the I_n cut-off on the fringe of *Onnia*, together with the identification of the position of the true girder, undoubtedly places *Onnia* in the Subfamily Marrolithinae (see Ingham 1974, p. 59; Hughes *et al.* 1975, p. 570). It is common for marrolithines to exhibit lateral fringe swelling and pit enlargement (seen in *Marrolithus*, *Marrolithoides*, *Costonia*, and some *Deanaspis*), although the tendency is by no means confined to this subfamily, having been independently developed in the Trinucleinae (*Telaemarrolithus*) and Hanchungolithinae (*Ningkianolithus*). Some *Onnia* taxa also exhibit this feature to a degree, none more so than *O. s. creta* subsp. nov. (described below).

Exfoliated specimens of *Onnia* in all our samples show areas of distinctive, closely spaced pitting (in reality they are spiculate areas on the underside of the test). One is a roughly rectangular area, situated immediately anterior to the anterior fossula, i.e. between the fossula and the innermost arc on the fringe. The other area is longer and crescentic in form and occupies a similar position with respect to the fringe but at the lateral periphery of the genal lobes (text-fig. 7G). These features may be areas of muscle attachment.

Onnia superba (Bancroft, 1929b)

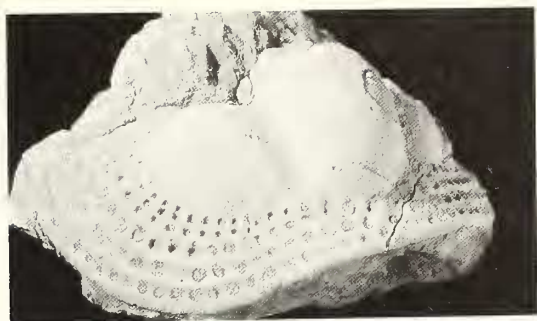
Plates 74–76; text-figs. 1, 3–7; Table 1

Emended diagnosis. Profile of upper lamella of fringe almost planar or variably convex, moderately declined. Arcs E_1 and I_1 complete, containing approximately 14–29 and 14–22 pits respectively. Arc I_n complete frontally and truncated posteriorly by I_3 which extends to the posterior margin but lacks about 3–10 pits mesially. Posterolaterally pits of I_3 , I_n and the anterior F pits may share sulci. I_2 complete posteriorly but with up to about 4 pits absent mesially.

Discussion. Our analysis of population samples of *Onnia* from the Onny River indicates that *O. superba* and *O. cobboldi* should not be maintained as separate species and that they are best viewed as subspecies. Both taxa were established by Bancroft in 1929 but although '*cobboldi*' was described earlier in his paper (1929b, pp. 92–94 cf. 95–96), as First Revisers under ICZN article 24(b) (1985), we here choose *superba* as the senior specific name. *Cryptolithus superbus* was designated the type

EXPLANATION OF PLATE 75

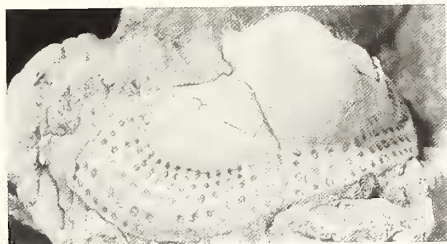
Figs. 1–11. *Onnia superba cobboldi* (Bancroft). Acton Scott Formation, *O. s. cobboldi* Local Range Zone, Onnian Stage, Onny River section, south Shropshire. All specimens testate unless otherwise stated. 1 and 2, HM A21761, oblique anterolateral and frontal views of cephalon, sample B, both $\times 3$. 3, HM A21732, oblique anterolateral view of cranium, sample B, $\times 3$. 4, HM A15158/1, 2, oblique views of two crania the smaller with reticulation on the mesial glabella and genal lobe, the larger smooth, sample D, $\times 4$. 5, HM A15184, oblique anterolateral view of partly exfoliated cephalon, sample E, $\times 3$. 6, HM A15183/1, oblique anterolateral view of portion of damaged cephalon showing subdued I_1 swelling, sample F, $\times 3$. 7, HM A15159/1, dorsal view of small, partly compressed cranium showing deeply pitted genal lobes and fine reticulation in narrow mesial band on glabella, sample D, $\times 9$. 8, HM A15178/1 oblique anterolateral view of part of cranium showing subdued I_1 swelling, sample F, $\times 4$. 9, HM A21742/1, oblique anterolateral view of cranium with very subdued I_1 swelling, sample B, $\times 4$. 10, HM A21734, oblique anterolateral view of incomplete cranium showing subdued I_1 swelling, sample A, $\times 4$. 11, HM A15159/2, oblique anterolateral view of partly exfoliated cranium showing slight I_1 swelling, sample D, $\times 6$.



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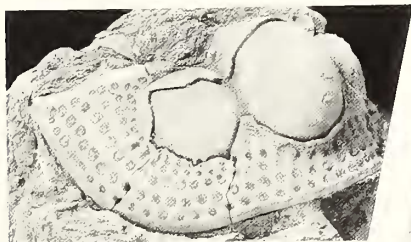
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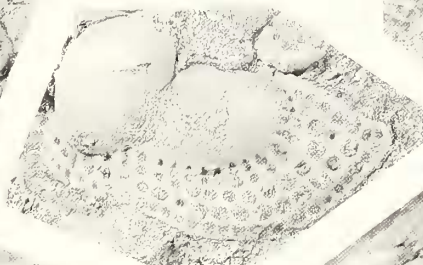
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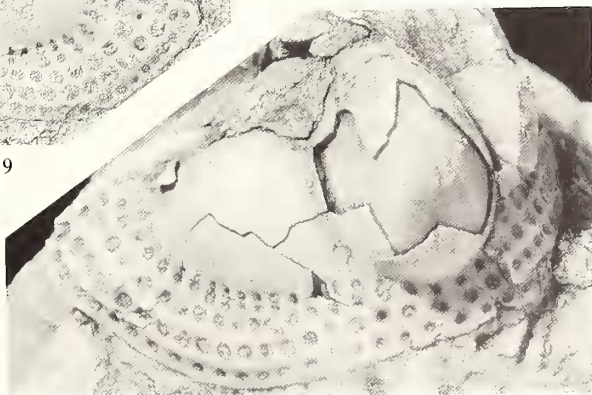
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species of *Onnia* by Bancroft in 1933 and it would be unduly disruptive to synonymize this well-established name with the hitherto less well-understood *O. cobboldi*. Moreover, topotype material of *O. superba* is widely dispersed through British and other museum collections. In the interests of stability therefore, we designate *O. superba* as the preferred species name.

Three subspecies of *O. superba* are recognized here. Dean (1960) gave full descriptions and synonymies of two of these, *O. s. superba* (as *O. superba*) and *O. s. cobboldi* (as *O.? cobboldi*), and thus only emended diagnoses are given herein. However, specimens of both subspecies are illustrated along with summary statistics of the fringe pit distribution. More detailed histograms of fringe data have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14034 (5 pages). Discussion of all three subspecies is given after the description of *O. s. creta* subsp. nov. It should be stressed, however, that Dean (1960) misinterpreted the first internal pseudogirder for the true girder; hence his descriptions refer to two E arcs, whereas only E₁ is actually present (see Hughes *et al.* 1975, p. 575).

Onnia superba superba (Bancroft, 1929b)

Plate 74; text-figs. 1, 3–5, 6C, D; Table 1

- 1929b *Cryptolithus superbus* Bancroft, p. 95, pl. 2, fig. 10.
 1933 *Onnia superba*; Bancroft, table 1 (*non* Dufton Shales = *O. pusgillensis* Dean, 1961).
non 1948 *Onnia superba* (Bancroft); Bancroft *in* Lamont, p. 416 (= *O. pusgillensis* Dean, 1961).
 1960 *Onnia? cobboldi* (Bancroft); Dean, pl. 19, fig. 1.
 1960 *Onnia superba* (Bancroft); Dean, pp. 133–136, pl. 19, figs. 4–6, 8, 9, 11, 13, 14.
 1960 *Onnia* aff. *superba* (Bancroft); Dean, pp. 136–137, pl. 19, fig. 10.
 1975 *Onnia superba* (Bancroft); Hughes *et al.*, pl. 9, fig. 107.
 1979b *Onnia superba* (Bancroft); Hurst, p. 210, fig. 36.

For complete synonymy see also Dean (1960, p. 133).

Holotype. An internal mould of a cephalon (BM In42070) from the upper part of the Onny Formation (level of sample V herein) (upper Onnian), cliff section, Onny River, south Shropshire.

Occurrence. Some complete specimens are known and disarticulated sclerites are abundant in the Onny cliff section and at some horizons in the river bed (when not covered by river gravels), in the upper 24 m of the type Onnian Stage. This distribution constitutes the *O. s. superba* Local Range Zone and extends across the boundary between the Acton Scott and Onny formations as recognized herein (text-fig. 1).

Emended diagnosis. External surface of glabella and genal lobe smooth except in small specimens. Fringe moderately declined, upper lamella only gently convex in early forms, more so in later populations. Arcs E₁ and I₁ complete, containing approximately 20–29½ and 15½–22½ pits respectively. Arc I_n contains about 12–17 pits, cut off posteriorly by I₃ which lacks approximately 3–9 pits mesially. Up to about 3 I₂ pits missing frontally.

Onnia superba cobboldi (Bancroft, 1929b)

Plate 75; text-figs. 1, 3–5, 6A; Table 1

- 1929b *Cryptolithus cobboldi* Bancroft, p. 92, pl. 2, figs. 6 and 7.
 1960 *Onnia? cobboldi* (Bancroft); Dean, pp. 128–132, pl. 19, figs. 3 and 12 (*non* fig. 1 = *O. superba superba*).
 1975 *Onnia cobboldi* (Bancroft); Hughes *et al.*, pl. 9, figs. 104–106.
 1979a *Onnia cobboldi* (Bancroft); Hurst (*pars*), pp. 204, 227 (samples 97, 98 only *non* 35, 99–102 = *O. superba creta* subsp. nov), fig. 16.11.
 1979b *Onnia cobboldi* (Bancroft); Hurst, p. 210 (*pars*), fig. 37.
 1983 *Onnia cobboldi* (Bancroft); Owen, pl. 34, figs. 1 and 5.

For complete synonymy see also Dean (1960, p. 128).

Lectotype. Selected by Dean (1960, p. 132), an incomplete cephalon (BM In42074) from the upper part of the Wistanstow Member of the Acton Scott Formation (Bancroft loc. Px = loc. B herein) (lower Onnian), Onny River section, south Shropshire.

Occurrence. Disarticulated sclerites are abundant at the type horizon and levels immediately above and below it. They are less common in the upper part of the *O. s. cobboldi* Local Range Zone (text-fig. 1). Complete specimens are extremely rare.

Emended diagnosis. External surface of glabella and genal lobes smooth in mature specimens, reticulated in small individuals. Upper lamella fairly steeply declined; fringe convex upwards, with some specimens also gently swollen along the lateral part of arc I_1 . Arcs E_1 and I_1 complete, comprising approximately $18-26\frac{1}{2}$ and $14-22\frac{1}{2}$ pits respectively. Arc I_n contains about 9–17 pits, cut off posteriorly by I_3 which lacks approximately 3–10 pits mesially. Up to about 3 I_2 pits missing frontally.

Omnia superba creta subsp. nov.

Plate 76; text-figs. 1, 3–5, 6B, 7; Table 1

1979a *Omnia cobboldi* (Bancroft); Hurst (*pars*), pp. 204, 227 (samples 35, 99–102).

1979b *Omnia cobboldi* (Bancroft); Hurst (*pars*), p. 210 (*pars*).

Holotype. A testate cephalon (HM A15087) from 14.8 m above the base of the Onnian Stage (sample H, text-fig. 1), upper Acton Scott Formation (*O. s. creta* Local Range Zone), Onny River section, south Shropshire.

Paratypes. Two cephalia (HM A15083, A15086/2), four cranidia (HM A15067/1, A15073/1, A15075, A15076), and a lower lamella (HM A15067/2). Other skeletal parts are not included here as the best specimens are from other sample horizons within the local range zone.

Occurrence. Disarticulated sclerites are common at four horizons within the 5 m of the *O. s. creta* Local Range Zone in the Onny River section. Complete specimens are known.

Derivation of name. From the Latin *cretus*, arisen; sprung/descended from; born of—referring to the possible derivation of this subspecies from the stratigraphically lower subspecies in the Onny River section.

Diagnosis. External surface of glabella and genal lobe variably reticulate, pitted, or smooth. Upper lamella of fringe markedly convex along very strong ridge-like swelling over lateral part of I_1 arc, beginning between about R_5 and R_9 beyond which the pits of I_1 are also enlarged. Arcs E_1 and I_1 complete, containing approximately 14–23 and 15–20 $\frac{1}{2}$ pits respectively. Arc I_n contains about 8 $\frac{1}{2}$ –16 $\frac{1}{2}$ pits, cut off posteriorly by I_3 which lacks approximately 3–10 pits mesially. Up to about 4 I_2 pits missing frontally.

Description. Cephalon almost semicircular in outline (excluding spines) but with sagittal length slightly more than half the posterior width. Strongly swollen (tr.), clavate, glabella achieves maximum width a short distance behind anterior fossula. Outer part of occipital ring ridge-like, directed abaxially downwards and forwards at about 45° to the sagittal line and defined anteriorly by deep, slot-like apodemal pit. Mesially, occipital ring differentiated from rest of glabella by only a slight break in slope and extended rearwards and slightly upwards as a stout spine whose sagittal length is equal to almost half that of preoccipital part of glabella. The rearward tapering of this spine is continuous with the general narrowing of rest of glabella. L1 developed as diminutive swelling marked anteriorly by small pit-like S1. Axial furrow broad and shallow bearing small but distinct fossula near its anterior end. Genal lobe strongly convex (tr., exsag.), quadrant shaped to reniform in outline. Posterior border narrow, convex (exsag.) directed transversely for a short distance before being moderately deflected rearwards and downwards to form posterior margin of fringe; inner part defined anteriorly by shallow furrow bearing posterior fossula distally. Long genal spines diverging gently at first but gradually becoming subparallel distally.

Many mature specimens and some smaller individuals have totally smooth glabella and genal lobes. Nevertheless, some mature specimens show surface sculpture. Pseudofrontal lobe of glabella in some specimens bears an ill-defined, broad, mesial strip of sculpture which is manifested either as a fine, occasionally coarser

reticulation or sometimes as a fine pitting in which pits may be clustered together in irregular groups of two to four, particularly towards front of glabella (Pl. 76, figs. 4–6; text-fig. 7A, B). This kind of pattern is occasionally also found on genal lobes, albeit in very subdued form. More commonly, sculpted specimens show fairly evenly spaced, shallow pits on genal lobes, except for their peripheral regions which are always smooth. Very small specimens have both glabella and genal lobes reticulated. An ill-defined glabellar node is situated at about the midlength of preoccipital part of glabella and at its highest point (sometimes difficult to detect on external surface of sculpted specimens, but invariably visible on internal moulds). Shape and position of spiculate areas on inner surface of test (see discussion of genus) in *O. s. creta* corresponds with those peripheral parts of genal lobes which are invariably smooth on outer surface.

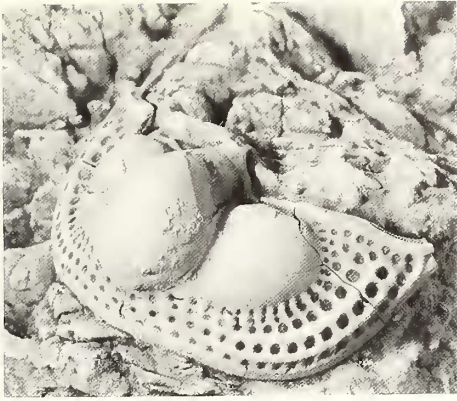
Fringe moderately steeply declined mesially, upper lamella increasingly more convex upwards abaxially. This is caused by development of an almost ridge-like swelling along course of arc I_1 , beginning between R_5 and R_9 (mean and mode 7, sample standard deviation 1, $n = 82$) such that inner part of fringe is gently declined, almost horizontal, or even concave upwards, and outer part, along E_1 , is so steeply declined that a substantial part is not visible in dorsal view. I_1 pits are noticeably enlarged along this inflated sector of fringe. Details of fringe pit number given on text-figs. 1, 3–5, table 1, and in the supplementary material in deposition. Arcs E_1 and I_1 complete, containing 14–23 and 15–20½ pits respectively in samples studied. I_n contains 8½–16½ pits and is cut off posteriorly by I_3 which contains 8½–14½ pits and lacks 3–10 pits mesially. 12–18 pits present in I_2 which lacks up to 4 pits mesially. F pit series begins between R_8 and R_{15} . Lower lamella fairly steeply declined, lacking any swelling equivalent to that along I_1 on upper lamella. Figured specimens (Pl. 76, fig. 2; text-fig. 7C, F) all show clearly the distinction between the true girder and the first internal pseudogirder.

Thorax typically trinucleid in plan, comprising six segments of which third and fourth occupy greatest width. Axis moderately convex but ill defined, occupying little more than one-fifth width of thorax throughout. Each axial ring is gently convex (sag., exsag.) and narrowest mesially, posterior margin arched forwards somewhat. Laterally, a shallow furrow originating in axial furrow at posterolateral extremity extends across each ring and shallows before becoming confluent with its counterpart. Articulating furrows sharply incised, defining simple articulating half-rings. Pleurae transverse for most of their length but deflected sharply posteroventrally towards their tips at a distinct fulcrum. Terminations blunt on all but first segment, which is shorter and more tapered to a rounded point. Pleural furrows broad and deeply impressed, confluent with axial articulating furrows, directed gently rearwards, deepest where they traverse the fulcrum but end abruptly just inside pleural termination. Convex posterior band thus tapers abaxially and ridge-like anterior band expands to fulcrum.

Pygidium broadly triangular in outline, larger specimens have sagittal length about 35 % of maximum anterior width, although smaller specimens proportionally longer. Posterolateral margins slightly sinuous in outline, with shallow concavities to either side of posterior, obtusely rounded termination. A posteriorly widening convex marginal band (sag., exsag.) extends around lateral and posterior margin. It is steeply declined and sharply recurved ventrally into a narrow doublure. Dorsally, the angulation between marginal band and pleural lobes is elevated as a narrow ridge. Axis only gently convex (tr.), occupying a little over one-fifth of maximum pygidial width anteriorly, relatively ill-defined by shallow axial furrows which converge gradually rearwards and become effaced before they reach marginal band. First axial ring well-defined both anteriorly and posteriorly by sharp furrows which bear apodemal pits abaxially; it is gently convex (sag.,

EXPLANATION OF PLATE 76

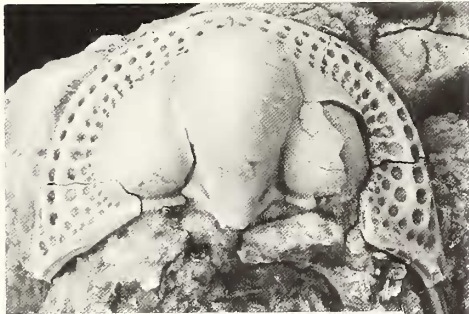
Figs. 1–9. *Omnia superba* (Bancroft) *creta* subsp. nov., Acton Scott Formation, *O. s. creta* Local Range Zone, Onnian Stage, Onny River section, south Shropshire. All specimens testate unless otherwise stated. 1 and 3, HM A15087, oblique anterolateral and dorsal views of holotype cephalon, sample H, both $\times 3$. 2, HM A15067/1, 2, oblique anterolateral view of cranidium and oblique ventral view of lower lamella, both paratypes, sample H, $\times 4$. 4, HM A21745, oblique anterolateral view of cephalon with reticulate glabella and pitted genal lobe, sample I, $\times 6$. 5, HM A21746, dorsal view of large cephalon with finely reticulate glabella and sparsely pitted genal lobes, sample J, $\times 2$. 6, HM A21747, oblique anterolateral view of portion of cranidium showing reticulate glabella and pitted genal lobes, sample J, $\times 4$. 7, HM A15075, oblique anterolateral view of paratype cranidium and incomplete thorax (pygidium present but not seen in this view), sample H, $\times 3$. 8, HM A15083, dorsal view of partly exfoliated paratype cephalon, sample H, $\times 3$. 9, HM A15086/2, oblique anterolateral view of paratype cephalon, sample H, $\times 4$.



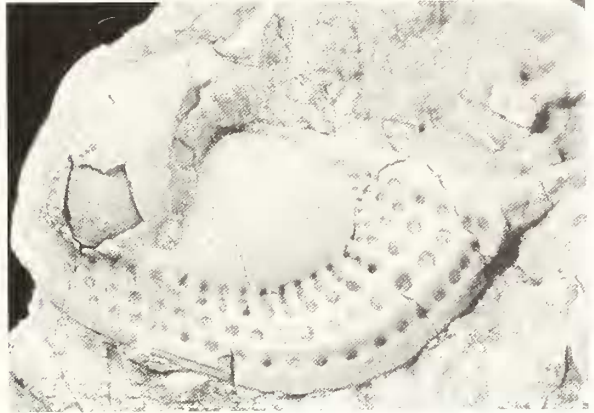
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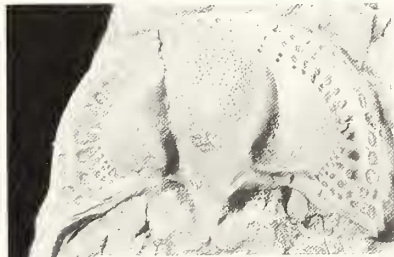
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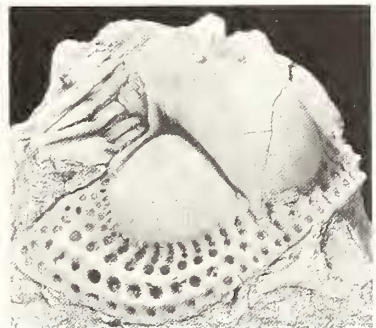
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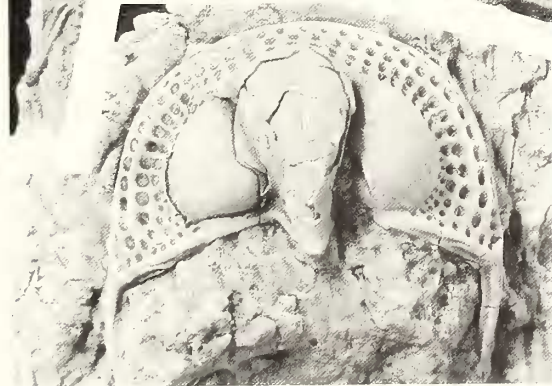
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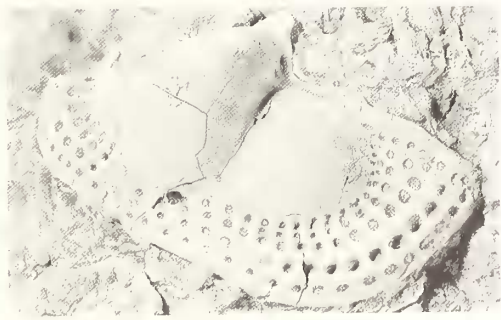
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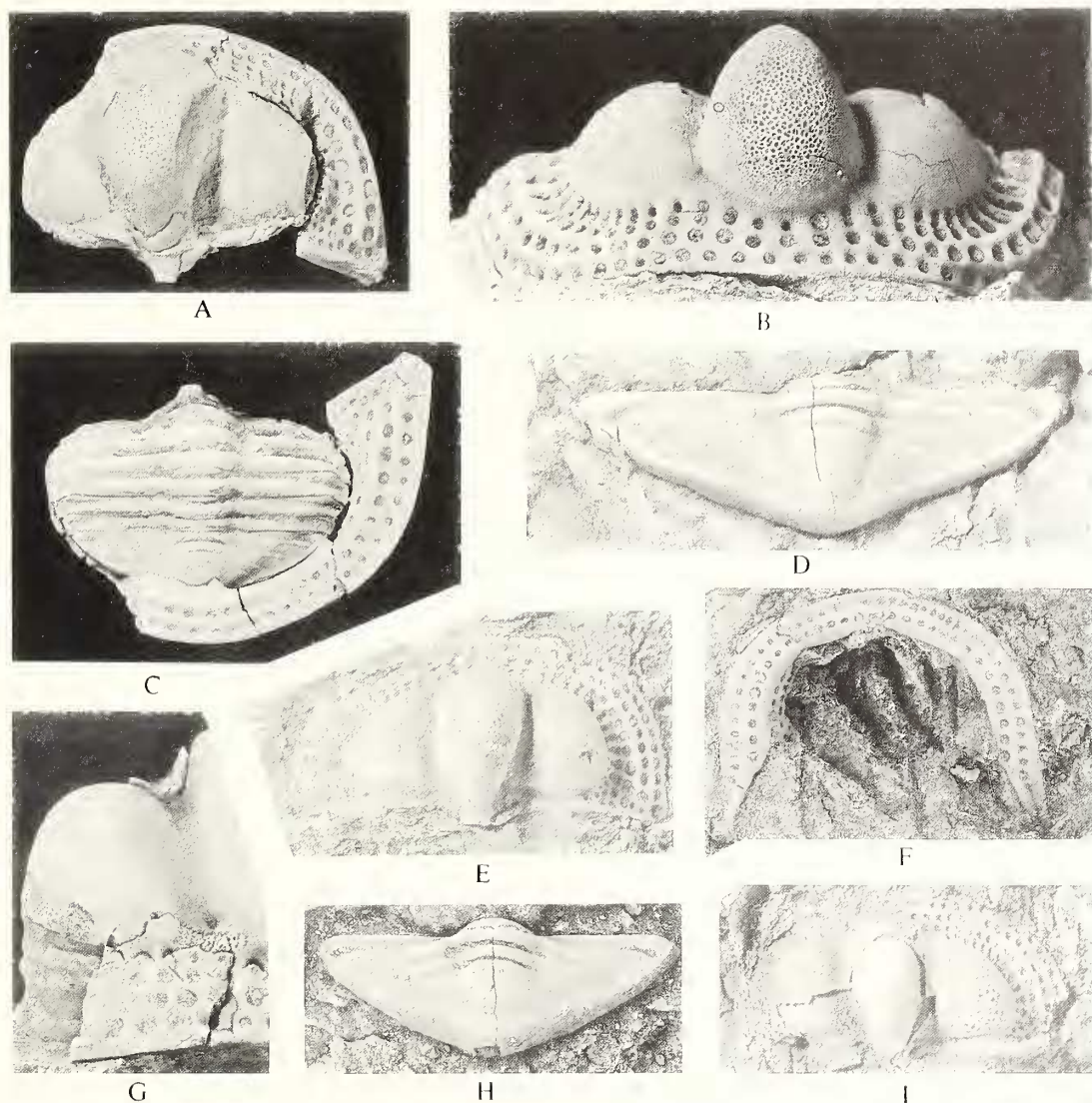
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exsag.) and gently arched forwards. Second ring a little more arched anteriorly but less well-defined posteriorly, the shallower furrow there still bears traces of apodemal pits abaxially. Successive rings progressively less well defined, particularly laterally but mesially they are a little clearer and may be impressed there as short, straight, transverse furrows with shallow depressions at their outer extremities. Seven or eight rings are present in all. Pleural lobes relatively depressed but gently convex adjacent to axis and gently concave abaxially. They are traversed by four distinct and slightly divergent pleural ribs, the anterior one or two following a slightly sigmoidal path towards submerged rim, which they almost reach. Ribs confluent with first four axial rings. Fifth pair of ribs barely discernible. Surface of pygidium largely smooth but marginal band and submarginal rim bear many fine anastomosing thread-like ridges.

Discussion of O. superba subspecies. The changes in pit number of successive populations of the subspecies of *O. superba* are shown in text-figs. 1 and 4 and table 1, whilst text-figs. 3 and 5 summarize the differences in pit distribution between the separate subspecies as a whole. These changes and differences are discussed in the section on 'Omnia in the type Onnian' (above). Suffice it to note here that the fringe pitting of *O. s. creta* subsp. nov. differs from that of the other two subspecies in its lower mean number of pits in each arc. This is especially true in arc E_1 where the lower part of its range extends well below the values of the other subspecies. *O. s. superba*, however, has a significantly higher mean value for arcs E_1 and I_3 than even *O. s. cobboldi*, with the former arc showing a marked overall increase in pits from early to late samples of the nominate subspecies. In addition to pit numbers, *O. s. superba* can usually be distinguished by the clearer separation of arcs I_2 and I_3 laterally. Moreover, the profile of the upper lamella ranges from near planar in early *O. s. superba*, through gently convex upwards in late *O. s. superba* and strongly convex in *O. s. cobboldi*, to the extreme convexity caused by the highly inflated lateral and posterior parts of arc I_1 in *O. s. creta*. Some specimens of *O. s. cobboldi* have a gentle swelling here but never as strongly developed as in *O. s. creta*.

Outside the Anglo-Welsh area, species of *Omnia* have been described from Caradoc and Ashgill rocks in north-west France, Iberia, Czechoslovakia, and Morocco (Hughes *et al.* 1975, pp. 574–575). Whilst it is clear that some of these peri-Gondwanan species are similar in many respects to *O. superba* subsp., most are in need of modern documentation and description. None has the markedly swollen posterior part of I_1 shown by *O. s. creta*. *O.* [or *Deanaspis*?] *vysočanensis* Přibyl and Vaněk, 1980 (pp. 268–269, pl. 3, figs. 1–3; text-fig. 1a, b), from the middle Caradoc Zahořany Group in Bohemia, has a very much broader glabella than is seen in the British species and there is a marked prolongation of the mesial part of the pygidial border. Details of the fringe are not clear from Přibyl and Vaněk's photographs, except that I_3 is absent at least anteriorly and anterolaterally. This arc is also missing in some illustrated specimens of *O. abducta* Přibyl and Vaněk, 1969, from the upper Caradoc Bohdalec Formation in Bohemia (see Přibyl and Vaněk 1980, pl. 6, fig. 6; Čech 1975, pl. 4, fig. 1). Examination of topotype specimens of *O. abducta* in the British Museum (Natural History) has confirmed this and has also shown that the pit distribution for most arcs lies well within the overlap in range shown by the three subspecies of *O. superba*, although the number of pits in E_1 is at or slightly beyond the upper part of the range in *O. s. cobboldi*. Like *O.* [D?] *vysočanensis*, the posterior margin of the pygidium of *O. abducta* has a sinuous outline.

The material described by Hammann (1976, p. 40, pl. 1, figs. 1–10; pl. 2, figs. 11–14; text-fig. 3; table 2) as *O.?* n. sp. aff. *grenieri* (Bergeron), from probable Ashgill strata (W. Hammann, pers. comm. 1984) in the eastern Sierra Morena, Spain, belongs in *Deanaspis*, a genus more typical of somewhat older strata. The girder and first internal pseudogirder are equally well developed anteriorly and anterolaterally, with the girder the more strongly developed beyond this. '*O. grenieri*', redescribed by Coates (1966, pp. 84–87, text-fig. 5a–e) on the basis of type and other material from the early Caradoc 'Vauville Formation' (now La Sangsurière Formation, Hammann *et al.* 1982, p. 8), also appears to have a moderately well-developed true girder frontally. This species also may be better placed in *Deanaspis*. It is at least broadly similar to *O. s. superba* and *O. s. cobboldi* in its cephalic and pygidial characters but better material needs to be described before a detailed comparison can be made.



TEXT-FIG. 7. *Onnia superba* (Bancroft) *creta* subsp. nov., Acton Scott Formation, *O. s. creta* Local Range Zone, Onnian Stage, Onny River section, south Shropshire. All specimens testate unless otherwise stated. A, C, HM A21738, dorsal and ventral views of cephalon in enrolled individual, sample J, both $\times 3$. B, HM A15073/1, frontal view of paratype cranium with fine glabellar reticulation, sample H, $\times 6$. D, HM A21748, dorsal view of pygidium, sample I, $\times 6$. E, HM A15076, dorsal view of paratype small cranium with reticulate glabella and genal lobes; note I_1 swelling subduced, sample H, $\times 9$. F, HM A21763, ventral view of lower lamella, sample I, $\times 3$. G, HM A21766, anterolateral view of part of damaged cephalon in which the right genal lobe has been stripped of test revealing, on internal mould, impressions of spiculate areas adjacent to anterior fossula and lateral margin of genal lobe, sample I, $\times 4$. H, HM A21743, dorsal view of pygidium, sample H, $\times 6$. I, HM A21740, dorsal view of partly exfoliated small cranium showing reticulate genal lobe and smooth internal mould of glabella, sample I, $\times 9$.

Onnia gracilis (Bancroft, 1929b)

Plate 77; text-figs. 1, 4, 8

- 1929b *Cryptolithus gracilis* Bancroft, p. 94, pl. 2, figs. 8 and 9.
 1960 *Onnia gracilis* (Bancroft); Dean, pp. 130–132, pl. 19, figs. 2 and 7.
 1962 *Onnia gracilis* (Bancroft); Dean, p. 84, pl. 8, figs. 12 and 13.
 1965 *Onnia gracilis* (Bancroft); Cave, pp. 282, 286, 287, pl. 12, figs. A, B, M, Q.
 1975 *O. gracilis* (Bancroft); Hughes *et al.*, p. 574.
 1979a *Onnia gracilis* (Bancroft), Hurst, p. 204 (samples 32–34, 36, 37).
 1979b *Onnia gracilis* (Bancroft); Hurst, p. 210.
 1983 *Onnia gracilis* (Bancroft); Owen, pl. 34, fig. 2.

For a complete synonymy see also Dean (1960, p. 130).

Lectotype. Selected by Dean (1960, p. 132), an incomplete cephalon (BM In42074) from the upper part of the Wistanstow Member of the Acton Scott Formation (= samples M and N herein) (middle Onnian), Onny River, south Shropshire.

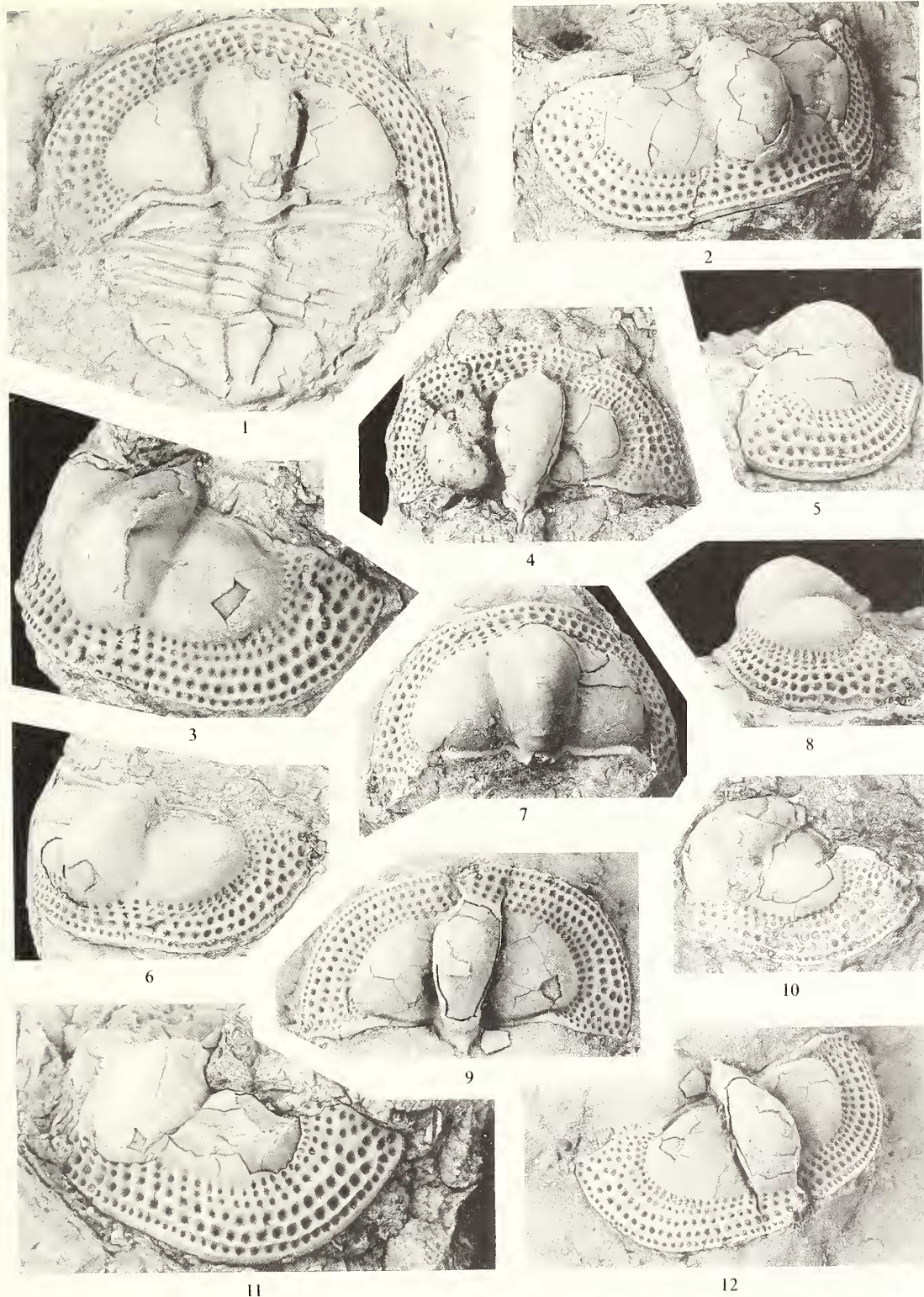
Occurrence. Rare complete specimens and abundant disarticulated sclerites occur in the 4.2 m of the *O. gracilis* Acme Zone in the Onny River section, and a few sclerites are known from the lowest part (sample N) of the overlying *O. s. superba* Local Range Zone. Bancroft's locality Pc was largely in the *O. gracilis* Zone but the presence of a few specimens of *O. s. superba* indicate that the lowest part of the overlying zone was also sampled. Our two samples M and N more precisely delimit the zonal boundary and demonstrate the nature of the co-occurrence of the two taxa. Disarticulated sclerites are also known from possible equivalents of the Onny River *O. gracilis* Zone at Welshpool (Cave 1965) and Cross Fell (Dean 1962). The species is also a rare component of strata of probable late Actonian age at Heath Brook near Cardington, south Shropshire.

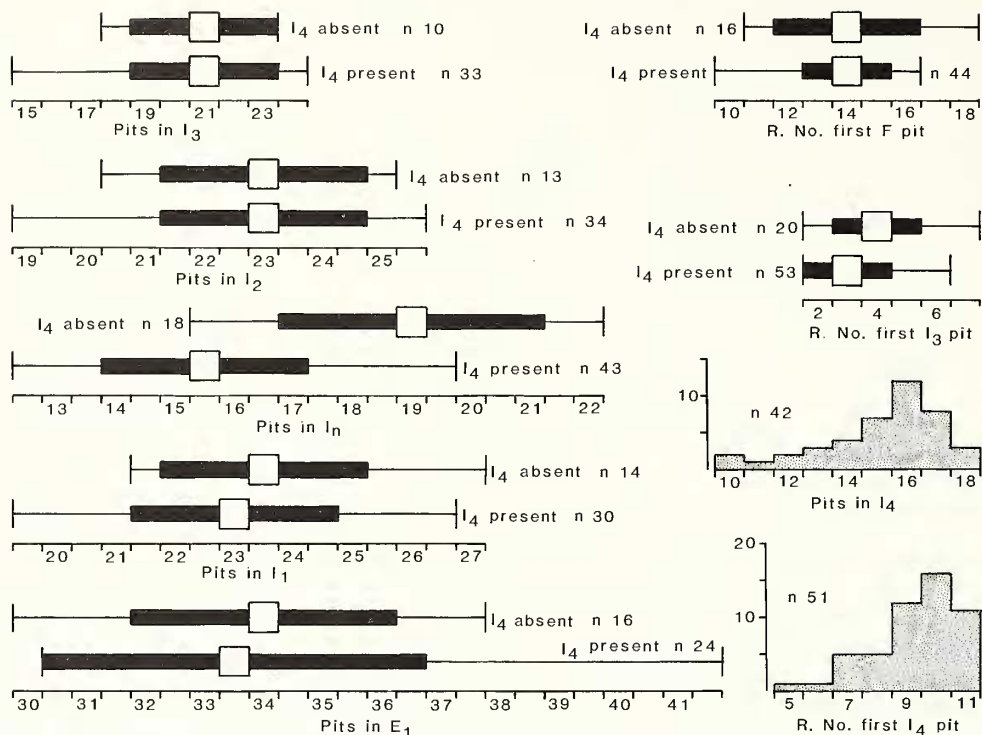
Emended diagnosis. External surface of glabella and genal lobe smooth. Fringe moderately declined, surface of upper lamella essentially planar. Arcs E_1 , I_1 , and I_2 complete, containing about $30\text{--}41\frac{1}{2}$, $19\frac{1}{2}\text{--}27$, and $19\text{--}25\frac{1}{2}$ pits respectively. Arc I_n of about $12\frac{1}{2}\text{--}22$ pits cut off posteriorly by either I_3 or (when present) I_4 which anteriorly lack 1–6 and (when present) 4–10 pits respectively.

Description. Dean (1960) gave an extensive description of *O. gracilis* which need not be repeated here save to enlarge upon and update his assessment of the fringe pitting. Number of pits in arcs E_1 , I_1 , and I_n in successive samples of *O. gracilis* are summarized in text-figs. 1 and 4, whilst text-fig. 8 shows total range of pits in these arcs together with arcs I_{2-4} and radius number of first pits in arcs I_3 , I_4 and F pit series. Two distinct morphs can be recognized based on presence or absence of arc I_4 . Moreover, when this arc is developed, it comprises at least ten pits. Like arc I_3 , it is always incomplete frontally. Range, mean, and one standard deviation on each scale of mean is shown for various fringe variables of the two morphs on text-fig. 8. For most features, there is little difference other than a slight increase in pit number when I_4 is absent. In the case of arc I_n , however, this increase is substantial. The three samples of *O. gracilis* from the *O. gracilis* Zone in the Onny River show a progressive decrease in percentage of specimens lacking arc I_4 , from 94 %

EXPLANATION OF PLATE 77

Figs. 1–12. *Onnia gracilis* (Bancroft), Acton Scott Formation, *O. gracilis* Acme Zone, Onnian Stage, Onny River section, south Shropshire. All except fig. 4 from Bancroft Collection loc. Pc (equivalent to our samples M and N, probably the former). All specimens testate or largely so unless otherwise stated. 1, BM In49032, dorsal view of paralectotype individual showing repaired damage to left side of fringe, arc I_4 present adjacent to I_n anterolaterally, $\times 3$, figured by Dean (1960, pl. 19, fig. 7). 2 and 5, BM In52014/2, oblique anterolateral and lateral views of cephalon lacking arc I_4 , $\times 3$. 3, BM In52010, anterolateral view of cephalon lacking I_4 , $\times 3$. 4, HM A15018, dorsal view of partly exfoliated crushed cranidium showing short occipital spine and I_4 present, sample L, $\times 2$. 6–8, BM In52014/3, oblique anterolateral, dorsal, and lateral views of cranidium, $\times 3$. 9 and 12, BM In52014/1, dorsal and oblique anterolateral views of somewhat flattened cranidium lacking I_4 , $\times 3$. 10, BM In52017/2, oblique anterolateral view of cranidium lacking I_4 , $\times 3$. 11, BM In52017/3, oblique anterolateral view of cranidium lacking I_4 , $\times 3$.





TEXT-FIG. 8. Summary of the fringe pit distribution in *Onnia gracilis* in the type Onnian Stage based on our own and Bancroft Collection specimens. Note that two morphs are present: one with and one lacking arc I_4 . Differences in other fringe features between these morphs are indicated by the illustration of the range, mean, and one standard deviation on each side of the mean.

(sample K, $n = 18$), through 91 % (L, $n = 43$), to 42 % (M, $n = 19$). Both specimens from lowest *O. s. superba* Zone have this arc as do all eight suitably preserved BM specimens from Cross Fell Inlier. Similarly, the four specimens from Welshpool have pits in I_4 .

Discussion. The broader fringe with more numerous E_1 pits (text-fig. 1), arc I_3 complete frontally, and (in some specimens) I_4 developed all serve to distinguish *O. gracilis* from the subspecies of *O. superba*. In addition, the mean number of pits in arcs I_{1-3} is greater than the numbers of pits seen in these arcs in *O. superba* but there is some overlap in total range (text-figs. 3, 4, 7). Only in the case of specimens lacking I_4 , however, is this marked difference seen in the mean value of pits in I_n .

Arc I_4 is invariably present in *O. s. pusgillensis* Dean, from the Dufton Shales of Cross Fell and equivalent Onnian strata in the Cautley Mudstones near Cautley (Dean 1961, 1962; Ingham 1974, pp. 60-63, pl. 10, figs. 1-18, text-figs. 20 and 21; see also text-fig. 2 herein). The complete development of I_2 frontally and, commonly, the greater anterior extension of I_3 (only about 3-5 pits missing frontally) also place the North of England form closer to *O. gracilis* than to *O. superba*. However, the number of pits in arcs E_1 and I_1 and the R number of the I_n cut off lie almost entirely within the range of the latter species, being $22\frac{1}{2}$ -31 ($n = 14$), 16-21 ($n = 15$), and 11-16 ($n = 14$) in the more abundant, better preserved material from Cautley (Ingham 1974, text-fig. 21). The gently convex profile of the upper lamella is also like that of late *O. s. superba* and some *O. s. cobboldi*. A numerical taxonomic analysis of British trinucleids by Temple (1981, text-fig. 9) showed that the species of *Onnia* plot close to each other in terms of the y_1 and y_2 axes of ordination, but

whereas '*gracilis*' has a low positive score on y_3 , '*superba*', '*cobboldi*', and '*pusgillensis*' have low negative scores. It must be stressed, however, that Temple's approach differs markedly from that used herein as it is based on a different set of attributes measured on small topotype samples of each taxon.

O. 's.' pusgillensis differs from both *O. superba* and *O. gracilis* in its much more subdued first internal pseudogirder which approaches the condition seen in *Deanaspis* where the girder and first internal pseudogirder are developed to about the same extent (Hughes *et al.* 1975, p. 573). Thus the North of England form shows a distinctive set of characters and is here given separate specific status. *O. pusgillensis* may have been derived either from *O. superba* or *O. gracilis* but its affinities are unclear.

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REFERENCES

- BANCROFT, B. B. 1929a. Some new genera and species of Strophomenacea from the Upper Ordovician of Shropshire. *Mem. Proc. Manchr. lit. phil. Soc.* **73**, 33–65.
- 1929b. Some new species of *Cryptolithus* (s.l.) from the upper Ordovician. *Ibid.* 67–98.
- 1933. *Correlation tables of the Stages Costonian-Onnian in England and Wales*, 4 pp. Blakeney, Gloucestershire (privately printed).
- 1945. The brachiopod zonal indices of the Stages Costonian to Onnian in Britain. *Jl Paleont.* **19**, 181–252.
- 1949. Upper Ordovician trilobites of zonal value in South-east Shropshire (edited by A. LAMONT). *Proc. R. Soc.* **B136**, 291–315.
- BERGSTRÖM, S. M. and ORCHARD, M. J. 1985. Conodonts of the Cambrian and Ordovician Systems from the British Isles. Pp. 32–67, table 1. In HIGGINS, A. C. and AUSTIN, R. L. (eds.). *A stratigraphical index of conodonts*. Ellis Horwood, Chichester.
- CAVE, R. 1965. The Nod Glas sediments of Caradoc Age in North Wales. *Geol. Jl*, **4**, 270–298.
- ČECH, S. 1975. Cranidial reticulation and functional morphology of the cephalic fringe in Trinucleidae (Trilobita). *Věst. ústř. Úst. geol.* **50**, 173–177.
- CISNE, J. L., CHANDLEE, G. O., RABE, B. D. and COHEN, J. A. 1982. Clinal variation, episodic evolution, and possible parapatric speciation: the trilobite *Flexicalymene senaria* along an Ordovician depth gradient. *Lethaia*, **15**, 325–341.
- COATES, A. 1966. Stratigraphie et paléontologie des synclinaux de Siouville et de Jobourg dans le Cap de la Hague (Cotentin, Normandie). *Bull. Soc. linn. Normandie*, (10), **7**, 77–103.
- DEAN, W. T. 1958. The faunal succession of the Caradoc Series of south Shropshire. *Bull. Br. Mus. nat. Hist. (Geol.)*, **3**, 191–231.
- 1960. The Ordovician trilobite faunas of south Shropshire, I. *Ibid.* **4**, 73–143.
- 1961. Trinucleid trilobites from the higher Dufton Shales of the Caradoc Series. *Proc. Yorks. geol. Soc.* **33**, 119–134.
- 1962. The trilobites of the Caradoc Series in the Cross Fell Inlier of northern England. *Bull. Br. Mus. nat. Hist. (Geol.)*, **7**, 65–134.
- 1963. The Ordovician trilobite faunas of south Shropshire, IV. *Ibid.* **9**, 1–18.
- 1964. The geology of the Ordovician and adjacent strata in the southern Caradoc district of Shropshire. *Ibid.* 251–296.
- GOULD, S. J. 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology*, **11**, 2–12.
- HAMMANN, W. 1976. Trilobiten aus den oberen Caradoc der ostlichen Sierra Morena (Spanien). *Senckenberg. leth.* **57**, 35–85.
- ROBARDET, M. and ROMANO, M. 1982. The Ordovician System in South-western Europe (France, Spain, and Portugal). *Publ. Int. Union geol. Sci.* **11**, 1–47.
- HAWLE, I. and CORDA, A. J. C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten*, 176 pp. Prague.
- HENNINGSMOEN, G. 1964. Zig zag evolution. *Norsk geol. Tidsskr.* **44**, 341–352.

- HUGHES, C. P. 1970. Statistical analysis and presentation of trinucleid (Trilobita) fringe data. *Palaeontology*, **13**, 1-9.
- 1971. The Ordovician trilobite faunas of the Bwlth-Llandrindod Inlier, Central Wales, Part II. *Bull. Br. Mus. nat. Hist. (Geol.)*, **20**, 117-182.
- INGHAM, J. K. and ADDISON, R. 1975. The morphology, classification and evolution of the Trinucleidae (Trilobita). *Phil. Trans. R. Soc.* **B272**, 537-607.
- HURST, J. M. 1978. A phenetic strategy model for dalmanellid brachiopods. *Palaeontology*, **21**, 535-554.
- 1979a. Evolution, succession and replacement in the type upper Caradoc (Ordovician) benthic faunas of England. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **27**, 189-246.
- 1979b. The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. *Bull. Br. Mus. nat. Hist. (Geol.)*, **32**, 183-304.
- 1982. Dalmanellid brachiopod phenetics. *Lethaia*, **15**, 342.
- INGHAM, J. K. 1966. The Ordovician rocks in the Cautley and Dent districts of Westmorland and Yorkshire. *Proc. Yorks. geol. Soc.* **35**, 455-505.
- 1970-1974. A monograph of the upper Ordovician trilobites from the Cautley and Dent districts of Westmorland and Yorkshire. *Palaeontogr. Soc. [Monogr.]*, Part 1 (1970), 1-58; Part 2 (1974), 59-87.
- 1978. Geology of a continental margin, 2: middle and late Ordovician transgression, Girvan. In BOWES, D. R. and LEAKE, B. E. (eds.). Crustal evolution in northwestern Britain and adjacent regions. *Geol. Jl Spec. Iss.* **10**, 163-176.
- and WRIGHT, A. D. 1970. A revised classification of the Ashgill Series. *Lethaia*, **3**, 233-242.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1985. *International Code of Zoological Nomenclature* (3rd edn.), 338 pp. University of California Press, London, Berkeley and Los Angeles.
- JOHNSON, A. L. A. 1981. Detection of ecophenotypic variation in fossils and its application to a Jurassic scallop. *Lethaia*, **14**, 277-285.
- JONES, C. R. 1987. Ordovician (Llandeilo and Caradoc) beyrichiocope Ostracoda from England and Wales. *Palaeontogr. Soc. [Monogr.]*, Part 2, 77-114.
- LAMONT, A. 1948. B. B. Bancroft's geological work in the Cross Fell Inlier. *Quarry Mgr's. Jl*, **31**, 416-418.
- LA TOUCHE, J. D. 1884. *A Handbook of the geology of Shropshire*, 91 pp. London and Shrewsbury.
- MALMGREN, B. A., BERGGREN, W. A. and LOHMANN, G. P. 1983. Evidence for punctuated gradualism in the Late Neogene *Globorotalia tumida* lineage of planktonic foraminifera. *Paleobiology*, **9**, 377-389.
- — — 1984. Species formation through punctuated gradualism in planktonic Foraminifera. *Science*, **225**, 317-319.
- MAYNARD SMITH, J. 1983. The genetics of stasis and punctuation. *Ann. Rev. Genet.* **17**, 11-25.
- MAYR, E. 1963. *Animal species and evolution*, 797 pp. Cambridge, Massachusetts.
- MURCHISON, R. I. 1839. *The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caernarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester and Stafford; with descriptions of the coalfields and overlying formations*, xxxii+768 pp. London.
- ORCHARD, M. J. 1980. Upper Ordovician conodonts from England and Wales. *Geologica Palaeont.* **14**, 9-44.
- OWEN, A. W. 1980. The trilobite *Tretaspis* from the upper Ordovician of the Oslo region, Norway. *Palaeontology*, **23**, 715-747.
- 1983. Abnormal cephalic fringes in the Trinucleidae and Harpetidae (Trilobita). In BRIGGS, D. E. G. and LANE, P. D. (eds.). Trilobites and other early arthropods: papers in honour of Professor H. B. Whittington, F.R.S. *Spec. Pap. Palaeont.* **30**, 241-247.
- 1985. Trilobite abnormalities. *Trans. R. Soc. Edinb. (Earth Sci.)*, **76**, 255-272.
- 1987. The trilobite *Tretaspis* at the Middle-Upper Ordovician boundary in Västergötland. *Geol. För. Stockh. Förh.* **109**, 259-266.
- PRIBYL, A. and VANĚK, J. 1969. Trilobites of the family Trinucleidae Hawle et Corda, 1847 from the Ordovician of Bohemia. *Sb. geol. Věd. Praha (Paleont.)*, **11**, 85-137.
- 1980. Neue Erkenntnisse über einige Trilobiten aus dem böhmischen Ordovizium. *Cas. Miner. Geol.* **25**, 263-274.
- SAVAGE, N. M. and BASSETT, M. G. 1985. Caradoc-Ashgill conodont faunas from Wales and the Welsh Borderland. *Palaeontology*, **28**, 679-713.
- TEMPLE, J. T. 1981. A numerical taxonomic study of species of Trinucleidae (Trilobita) from the British Isles. *Trans. R. Soc. Edinb. (Earth Sci.)*, **71**, 213-233.

WHITTINGTON, H. B., DEAN, W. T., FORTEY, R. A., RICKARDS, R. B., RUSHTON, A. W. A. and WRIGHT, A. D. 1984. Definition of the Tremadoc Series and the series of the Ordovician System in Britain. *Geol. Mag.* **121**, 17-33.

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Note added in proof. In his recent review of British trilobites, Morris (1988, p. 155) has drawn attention to an abstract written by us for the Palaeontological Association's Evolutionary Case Histories Symposium in 1983. In that preliminary report about our work on *Ommia* we (as Ingham and Owen) suggested the name *O. cobboldi creta* for the taxon here described as *O. superba creta*. The collection of abstracts for the meeting was not paginated. It was intended purely for the information of likely delegates to the conference and was distributed as an annexe to the *Palaeontological Association Circular*. Since the subsequent publication of the 1985 ICZN Code, the *Circular* includes a taxonomic disclaimer confirming that it is not valid for taxonomic purposes. Thus the abstracts were not 'for the purpose of providing a permanent scientific record' (see Article 8(a)(i) of the 1985 International Code of Zoological Nomenclature). Indeed, amongst the papers in the formal publication arising from the meeting (Cope and Skelton 1985) there is, for example, a formal abstract (op. cit. p. 185) by another author which was intended to be a permanent record of his work. No type specimen (or even museum collection, cf. Morris 1988, p. 155) was indicated by us. Moreover, owing to a typographical error in our abstract, the only phrase which could be construed as a taxonomic 'description or definition' (see Article 13(a)(i)) is nonsensical and reads 'later specimens have the outer parts of arc I situated on a distinct ridge' [there are four or five I arcs present in all the Shropshire specimens of *Ommia*]. Thus we consider *O. c. creta* to be a *nomen nudum* and *creta* therefore is an available name. The formal establishment of *Ommia s. creta* is in the present work.

COPE, J. C. W. and SKELTON, P. W. (eds.). 1985. Evolutionary case histories from the fossil record. *Spec. Pap. Palaeont.* **33**, 202 pp.

MORRIS, S. F. 1988. A review of British trilobites, including a synoptic revision of Salter's Monograph. *Palaeontogr. Soc. [Monogr.]*, 316 pp.